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This report first presents an outline of a number of themes that arose during the meeting and the comments by the various participants as to how their work fits into the general themes. The general themes are followed by a more detailed discussion of the work planned by each research group over the next year as part of their ONR supported project.

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WORKSHOP ON FISH HEARING - 1994
MAY 17, 1994

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The 1994 meeting took place on Saturday May 17, 1994 at the Washington-Dulles Marriott Hotel. The program took the form of presentations by the individual research groups as to the nature of their proposed work. This was followed by a discussion of the work and an outlining of general themes that encompassed the work being done in the various research programs and the context for cooperation and collaboration across research groups..

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BACKGROUND - NAVY RELEVANCE OF WORK ON FISH BIO-ACOUSTICS

The Navy has a need to detect, classify and localize objects such as mines and submarines, in the underwater environment. These tasks must be performed quickly and accurately under a wide variety of environmental conditions. Since electromagnetic energy does not propagate well in the ocean, hydrodynamic signals, usually in the form of sound, must be used. This often becomes an extremely difficult task due to various noises which hamper the detection of signals of relevance. The interfering signals can include self-generated noise and ambient noise (both propagated sound pressure noise and incompressible flow noise) from exogenous sources, like marine life, man-made sources, wind, currents, etc., and flow noise, the latter dominating at high speeds of a vessel. To date, the towed array is the only relatively effective solution to date to enable the detection of relevant signals in the presence of noise. The length of these arrays and the fact that they are physically removed from the platform (e.g., ship or submarine) enables them to cope with the noise at low speeds.

However, while relatively effective in open water, towed arrays often cannot be deployed in shallow water. Significantly, shallow water is currently the environment of highest interest to the Navy! As a consequence, the Navy will have to develop some way to function without the towed array in order to detect relevant signals in shallow water. *Such new methods might include different arrays and/or different array-processing strategies.*

It is very significant to problems encountered by the Navy that fish deal with many of the same acoustic problems as does the Navy. Sound is the best way for fish to communicate over long distances with a directional signal, and they have to be able to extract relevant signals in the presence of ambient noises and self-generated noises, particularly when they are moving at high speeds or maneuvering in tight spaces, such as on coral formations. Numerous species of fish inhabit shallow waters where they encounter additional propagated sound pressure and incompressible flow signals such as waves and surf. *Fish are able to deal successfully with noise in all environments using a very small aperture (with no means for augmenting it) and a very small signal processor (the brain).*

It may be of critical importance to the Navy that fish are likely to have evolved entirely different and as yet unimagined methods for detecting and localizing underwater objects in the presence of noise. *This could be of critical importance to the Navy!* Certainly, the detectors used by fish (ear and lateral line) are very small and compact, and yet it is apparent from many previous studies that fishes

are able to detect and localize very low level signals, even in the presence of very substantial masking signals. Thus fish may use better transducers and signal processing approaches and perhaps even exploit entirely different aspects of the signal and noise field than those currently used by the Navy. Navy scientist and engineers may be able to learn quite a bit from underwater detection systems which have been undergoing "engineering development" for 300,000,000 years!

As discussed in the next section, the thrust of the work being done by this group of investigators is to carefully examine the mechanisms by which fish detect and process acoustic signals. The work is built upon several decades of investigations that have provided a wealth of behavioral, physiological and morphological data that has demonstrated the diversity and capabilities of fish systems in question for detection and processing of signals. We are now in a position to ask questions critical to the Navy for dealing with complex detection problems in shallow water environments - and to develop computational models for detection and localization that should provide real insight into how fishes deal with the complex acoustic environment in deep and shallow waters.

GENERAL THEMES

A number of themes permeate the work of the various investigators on this project, and the meeting served to highlight these. The combined studies will clearly provide a broad understanding of significant aspects of signal detection and processing by fishes. The themes brought out at the meeting and which permeate the work being undertaken quite closely address issues of general signal detection and analysis that go beyond questions of how fishes function to questions of how any type of sensor might function in order to extract the maximum information about its acoustic environment. While no individual theme was addressed by every research group, each theme was encompassed by at least several of the investigators. These themes were:

Sound field disturbance detection: How do fishes detect objects in their environment that produce scattering of the sound field? This is a passive detection system as opposed to active detection of objects using emitted energy.

Particle motion/pressure sensory coupling: How do fish combine and use pressure signals and particle motion signals to obtain the maximum amount of information about their environment? This is a fundamental issue for determination of sound source direction, and it may be relevant for the general issue of extraction of signals in the presence of various types of noise.

Signal enhancement and noise filtering: How are sensory structures and CNS circuits designed to sharpen signals and reject unwanted noises? This is basically a problem of increasing the signal-to-noise ratio.

Cross-modal processing: What are the interactions between the various detectors (in fish, the ear and lateral line) and how does this enhance the ability of fishes to detect and respond to signals as opposed to having a single detector system? Fishes use several different types of detectors (ear and lateral line) and several processing systems (for the ear, lateral line and Mauthner cell). How is this information combined or integrated by the CNS circuits like the Mauthner cell complex to provide a picture of the acoustic environment?

Array processing: Processing of information that is detected through a spatial array of multiple detectors to extract information about the signal (e.g., direction, distance).

Computational approaches: What kind of algorithms are used by fishes in processing of acoustic information? Can these algorithms be modeled?

As outlined in the discussion of each theme by individual investigators, the thrust of the work being supported by ONR gets directly at questions of detection and processing of low frequency directional signals. The work being done by this group of investigators focuses on the two hydrodynamic/acoustic sensory systems available to fish, the ear and the lateral line, and on the CNS circuits that use information from these sensors to mediate directional behaviors, such as those involved in locating prey or avoiding predators. One such circuit is the Mauthner cell complex that receives input from the ear and the lateral line, and outputs motor commands to produce very rapid escape responses. Each of the two sensory systems, in combination with the various CNS circuits, provides the fish with the ability to respond to directional signals. However, various CNS circuits deal with different localization needs. For example, the M-cell functions for extremely rapid directional

escape response from predators (within milliseconds of initial detection), while there are certainly other, currently unknown, circuits, that mediate orienting and strike (feeding) responses towards prey. Studies of the M-cell provide not only information on the way in which fishes respond rapidly and directionally to a stimulus, but provide potential insight into the algorithms involved in processing information from the ear and the lateral line.

Because the ear and lateral line respond to acoustic and hydrodynamic fields differently, the kinds of information that can be extracted by each differ, and are yet complimentary. For example, the lateral line responds to spatial nonuniformities in the acoustic/hydrodynamic field very close to the source, and, as such, is capable of forming very precise hydrodynamic images of nearby vibrational sources or stationary obstacles in the environment. The ear does not depend on spacial nonuniformities close to the source, but can respond to sources at greater distances, as long as the fish's body is accelerated by the source. Thus, the ear is more valuable in detecting sources at greater distances, but may not be as good as the lateral line in extracting detailed information about the size, shape or precise location of the source. In essence, one can view the systems as working together to provide an overall image of the fish's acoustic/hydrodynamic environment to enable the fish to respond rapid and directionally to a wide range of potential predators and prey.

From the perspective of the Navy, each of these detection capabilities in a fish has parallels for underwater detection (e.g. early detection and avoidance, hydrodynamic imaging for navigational purposes, and passive detection of submarines). Very significantly, the sensory systems in fishes are very small and highly compact. Moreover, the CNS has evolved quite efficient algorithms for signal conditioning and noise rejection strategies that enhance the ability of fish to respond accurately and rapidly to a signal. In addition, fishes have algorithms that enable them to produce directional behaviors that respond to the environment around them. While we know very little about the algorithms used by fishes in these processes, it is possible that there is considerable overlap between them and that they combine input from both ear and lateral line.

In order to have applicability to Navy problems, it is critical to get further data on the sensory systems being studied. This will provide a better understanding of the detection capabilities, stimulus parameters, and response characteristics of the endorgan(s) to more precisely model the function of each system. Once we have these data, we will be able to look at the systems in toto to help us understand the contributions each makes to the overall capabilities of fish to detect low frequency sounds, and determine sound source direction and distance.

In the following sections, each of the P.I.'s presents ideas on the applicability of his/her research project to these themes.

Sound field disturbance detection

Rogers: I believe that our Mauthner Reflex work will have relevance to the detection and localization of submarines via acoustic transients and that our work on scattered ambient noise has application to the passive detection of mines.

Eaton: We have recently published on how fish avoid obstacles while turning away from aversive acoustic stimuli that elicit escape. As part of our experimental protocol in this ONR study, such observations can be readily done on blinded fish and fish with the lateral line pharmacologically blocked, or with both sensory systems inactivated. This will reveal the extent to which fish have the capability of analyzing the acoustic signal in avoidance of solid obstacles in the environment.

Hastings: Detection of a sound field disturbance is initiated by the transduction of acoustical to electrical energy in the periphery. At present, the understanding of this transduction process is descriptive at best. Our project will develop an understanding of the microelectromechanical details in the peripheral transduction path to more fully answer the question as to how a sound field disturbance is transformed into a pattern of neural activity that travels to the central processor. Moreover, the mathematical model that will be developed as part of our program could be used to further investigate the response of this system to all different types of sound field disturbances.

Particle motion/pressure sensory coupling

Eaton: We will be directly studying this issue in evaluating the neural processing of directional sound information in the acute goldfish preparation. We assume that there is much less separation of the pressure and particle motion components at the sensor level in hearing non-specialists such as

the oscar in comparison with specialists such as the goldfish. The implication, based on our present conception, is that the mixture of pressure and particle motion components in the non-specialists should be a more complex input which would require more complex neural processes to disambiguate these components for directional determination. One possibility is that the non-specialist could not perform the directional analysis as quickly or as accurately as a hearing specialist. Therefore, a neurophysiological and neuroethological comparison of the directional acoustic processing by the Mauthner system in a non- specialist will be necessary.

Hastings: The peripheral auditory system of bony fishes simultaneously detects both acoustic particle motion and pressure. The sensory coupling begins in the periphery. Our work will decompose the response of the periphery to both inputs, and examine the bioelectromechanics of the coupling. The response will be examined experimentally as well as analytically. The mathematical model that will be developed as part of our program will provide a foundation for hardware development of a dual acoustic pressure and particle velocity sensor.

Sensory enhancement and noise filtering

Coombs: Dr. John Montgomery (co-investigator on this ONR grant) and Dr. David Bodznick have shown evidence for adaptive filters in first-order medullary nuclei of both the electrosensory system of elasmobranchs and the mechanosensory lateral line of a teleost fish (the scorpion fish). Whereas primary afferent fibers show robust responses to electric and flow field changes due to ventilation, secondary cells in medullary nuclei show responses that adapt over time to ventilatory signals or to signals paired with ventilatory cycles. They have a model for how this adaptive filter works, based on processing that occurs in the dorsal neuropile of these nuclei. This is just one example of how neural circuits in the CNS can enhance the delectability of the signal by filtering out unwanted noise, in this case, that due to the animal's own movements. By comparing response properties of peripheral fibers with those of secondary cells to sources that change location, Dr. Montgomery and I will continue to examine ways in which local CNS circuits may enhance the ability of the lateral line system to extract information about source location.

Cross-modal processing

Coombs: The main focus of this project will be lateral line, although it may easily turn out that we will be able to study both lateral line and inner ear contributions to the orienting response of the mottled sculpin. Results to date, however, suggest that the behavior relies heavily, if not exclusively, on the lateral line system. Based on what we know today, it appears that the ear provides crude information on the location of sources at distances greater than one or two body lengths, whereas the lateral line gives you more precise information on source location at closer ranges. This seems to be the main way in which information from the two systems are used in locating sources. We do not know, however, how or if the two systems are behaving synergistically when the source is within the distance range of both - that is certainly something that we will investigate.

Eaton: In our experiments, we will be determining the involvement of the lateral line in determining sound source direction in the near vicinity of the fish. The lateral line may provide important information to the auditory system for solution of the XNOR. If this turns out to be the case in our behavioral studies, we will evaluate this role by providing lateral line stimulation in the acute preparation and then pharmacologically blocking this system as in our behavioral studies.

Hastings: Although we are not directly addressing sensory fusion in our program at this time, our mathematical modeling of the bioelectromechanics of the periphery could readily be extended to include the lateral line. Inclusion of the lateral line in the mathematical model would provide a computational means to investigate the division and overlap in the roles of the lateral line and inner ear in auditory ability. Moreover, the extension would provide a basis to examine the signal processing necessary for extraction of nearfield and farfield acoustical signals detected by the acoustico-lateralis system.

Popper et al: Anticipating collaborations with Hastings on peripheral function, the results of our physiological studies of directional hearing, combined with Hastings biomechanical models, should provide the basis for a comprehensive model of peripheral processing with regard to the ear. These data will provide input that will be needed in modeling and understanding the interactions between the ear and lateral line.

Array processing

Coombs: This will be one of the major focuses of our grant. We will essentially be testing the hypothesis that source location and distance is encoded by the pattern of excitation along differently oriented arrays of lateral line receptors on the head and trunk of the fish. Computational modeling approaches will be used to predict the pressure gradient pattern expected to stimulate the lateral line system as a function of source distance, location and axis of vibration. Physiological approaches will be used to reconstruct the pattern of excitation for neuromasts located on different parts of the body. Although array processing by the lateral line system may be viewed as being severely limited because of its short distance range, it should be pointed out that the distance range of the lateral line is limited only by the length of the receptor array and the distance between receptors. Thus, any principles for array processing that we might establish for the lateral line system could be scaled up to increase the distance range.

Eaton: We are already looking at algorithms that are designed to extract information from hair cell arrays and we can easily add lateral line arrays if necessary. We are using a cosine representation for which, we note, David Touretzky (Carnegie-Mellon University) has already developed neural algorithms for performing vector operations. We have already begun to consider how Touretzky's analysis might be useful in the escape system.

Popper et al.: We will be investigating the responses of single cells as well as of different endorgans of the ear in detection of directional signals. It is more than likely that the combined inputs from the various receptor arrays will be necessary in order for a fish to get sufficient data on the direction of a signal. In essence, we will be analyzing the input from multiple accelerometers (multiple endorgans) that provide input for directional defemination.

Computational approaches

Coombs: We will be using a limited computational approach to analyze behavioral results and to predict pressure gradient patterns to the lateral line as a function of source location, distance and axis of vibration. Dr. Montgomery will also do some neural net modeling of strategies used for source localization by the lateral line. A computational approach used to predict pressure gradient patterns to an array of lateral line receptors will be used to generate the input to a generalized neural network (Neural Net Toolbox from MATLAB). The idea is to ask the network to learn the target position and to determine what information the network uses to localize the target. This approach can then be used to look at the effects of lesions (i.e., removing receptor elements in the array) on the network output.

Eaton: We already have a computational system which, if attached to right sensors, would be able to decide right from left of a transient sound source. Given the right sensors, one could make this network out of silicon. Having the right sensors, we could easily train a net to do this task. We (and Rogers) have provided an easily implemented algorithm for processing this kind of signal. Our neurophysiological experiments are designed to test the validity of the computational model. In addition our experiments will provide new information about how the real problem is solved. These are complexities that are required to solve the problem in a real fish (or network) but which are not yet part of the overall theory in its general form.

Popper et al.: The thrust of our work is to develop a computational model for sound source localization. Using an earlier model (Rogers, Popper, Hastings and Saidel) as a starting point, we will obtain data on the specific response characteristics of the endorgans of the ear and develop models for sound source localization. Earlier models (including our own) lacked physiological response data and this is a significant weakness to those models. The new (or refined) model we develop will be unique in being based upon extensive physiological data and well as from the anatomical data on neuronal innervation of the ear and the projections of neurons to the brain that will be derived from the work. In addition, the model will include data we are now generating on the receptors in the ear of fishes. Again, such information has not been heretofore taken into account in earlier models (including our own).

RESEARCH AREAS OF INDIVIDUAL INVESTIGATORS

LOCALIZATION OF LOW FREQUENCY HYDRODYNAMIC SOURCES BY FISH

P.I.: Sheryl Coombs, John Montgomery, Ruth Conley

The objectives of this project are to: (1) identify the behavioral strategies and sensory cues used by fish in localizing nearby, low frequency hydrodynamic sources; (2) determine how source location is encoded by the lateral line system - a spatial array of pressure gradient receptors; and (3) determine how the peripheral representation of source location is enhanced or transformed by neural circuits in the central nervous system.

To achieve these goals, we are using a combination of behavioral, physiological and computational approaches. Behavioral approaches involve videotaping the natural orienting behavior of a freshwater fish, the mottled sculpin, to a low frequency (10 - 50 Hz) sinusoidally-vibrating sphere. The same stimulus source and fish species is used in physiological approaches, which involve extracellular recording techniques to measure the responses of single lateral line nerve fibers and brainstem neurons to sources varying in location. In collaboration with Mardi Hastings, a computer model of the dipole flow field will be used to predict the pattern of pressure gradients that would occur across an array of lateral line receptors for different source locations.

Over the next year we will obtain behavioral data on the normal localization behavior of fish with lateral line and auditory systems intact. Pathways followed by blinded fish to dipole sources will be videotaped and the relationship between the fish and both the source and the flow field will be measured for each step in the pathway. We will determine which, if any, of the following hypotheses best describe the strategies used by fish in localizing the source: (1) fish maintain constant angles with the flow lines, (2) fish align their bodies along the flow lines, (3) fish move in a direction that produces increasing positive pressure gradients along the head and near zero pressure gradients across the head.

Physiological experiments will measure response patterns from posterior lateral line nerve fibers innervating the trunk canal of the mottled sculpin. Response patterns will be determined for a source that continuously changes location along the rostral-caudal axis of the fish for sources with different vibration axes and at different distances and elevations.

Using the actual anatomical dimensions of the mottled sculpin lateral line system and the stimulus dimensions used in behavioral and physiological experiments, we will also model the pressure gradient patterns expected along the trunk canal of this fish. Modeled predictions will be compared with physiologically-measured response patterns to determine how source location might be encoded by the peripheral nervous system.

Follow-up studies in the second and third years will determine how localization behavior is altered when the inner ear or portions of the lateral line is eliminated and how response patterns of secondary (medullary) cells differ from peripheral nerve fibers.

The Mauthner System Model for Directional Hearing in Fish

P.I.: Robert C. Eaton

We propose to study the problem of sound localization in fish by analyzing the neural mechanisms of sound avoidance responses triggered by the Mauthner system. This is the common startle response seen in aquarium fish when the glass is tapped. Over millions of years of evolution fish have developed the ability to detect sound source location, yet the underlying mechanisms are not understood. Insight into such processes may be of material benefit in the design of compact and efficient underwater sound location detectors.

Theoretical and experimental studies support the phase model for sound source localization by fish. The Mauthner system is advantageous for applying the phase model to neurobiological study because this system is already well described and it is accessible for neurophysiological methods. Moreover, the basic neural decision is very simple: the fish merely turns away from the sound source. When one of the Mauthner cell fires, we know that the fish has perceived the sound as coming from the same side of the body. Thus, by using the Mauthner system, we are studying known processes in identified neurons and we thereby reduce the problem of sound source localization to manageable proportions.

We have recently developed a new logical tool, the XNOR model, which can be used to analyze how the neural components of the Mauthner system interact to determine the direction of sound sources. We propose to analyze the XNOR model in three types of experiments:

1) Neuroethological studies will be done to demonstrate Mauthner firing to directional sound sources, to show the possible involvement of the mechanosensory lateral line and to characterize the

sounds made by two typical aquatic predators during attacks on fish.

2) Neurophysiological experiments will be done on the primary acoustic afferents that activate the Mauthner cell, on the PHP inhibitory neurons that control Mauthner threshold, and on the Mauthner neurons themselves. These studies are intended to show which logical components of the XNOR model are mediated by these various neural elements.

3) Neurocomputational models trained with backpropagation will incorporate the above findings in the development of appropriate neural models of sound localization by the various elements of the Mauthner system. These models have already been instrumental to us in developing the XNOR model.

By using three levels of experimental analysis, from behavior to neural computation, we are bringing a comprehensive evaluation to the issue of directional sound processing and thereby should be able to provide new knowledge about the underlying mechanisms. These are particularly feasible experiments because the requisite methods and techniques are already used in the laboratory or are readily available elsewhere. Therefore, the proposed studies have a high probability of success.

MECHANICAL RESPONSE OF THE PERIPHERAL AUDITORY ORGANS TO LOW FREQUENCY SOUND

P.I.: Mardi C. Hastings

The overall objective of our project is twofold: (1) to experimentally examine the mechanical response of the peripheral auditory organs *in vivo* to acoustic pressure and particle velocities at frequencies down to 10 Hz; and (2) to determine the role of the periphery in auditory capabilities such as source localization and frequency analysis. Our approach follows parallel experimental and analytical paths. To examine the mechanical response, fish will be anesthetized, suspended in a flexible waveguide, and exposed to a traveling acoustic plane wave, or to the node (acoustic particle velocity stimulus) or antinode (acoustic pressure stimulus) of a standing wave. The spatially distributed motion of the peripheral auditory organs in response to the low frequency sound wave will be measured using a noninvasive system based on phase-modulated continuous wave ultrasound developed by Rogers and Hastings in a previous ONR project. Frequency response measurements of each peripheral auditory organ will be made along two orthogonal axes with the fish oriented both longitudinally and transverse with respect to the acoustic wave. These measurements will be repeated with the swimbladder deflated, and with two different species: *Carassius auratus*, a hearing specialist and *Astronotus oscellatus*, a non-specialist. To realize the second objective, a transfer matrix mathematical model of the peripheral bioelectromechanics will be developed in parallel with the experimental measurements to identify and examine the mechanisms and paths involved in the transduction process. Correlation of the mathematical model with the measured data will allow the model to be used to investigate the role of the periphery in auditory capabilities.

Except for the swimbladder, no frequency response data for the peripheral auditory organs exists at frequencies below 500 Hz because of the difficulty of creating low-frequency acoustic stimuli in a confined space. Thus far we have completed the design of a low frequency waveguide and the experimental apparatus, and identified the exact equipment required for the noninvasive vibration measurement and fish positioning systems. In addition, we have completed the first one-degree-of-freedom transfer matrix mathematical model of the peripheral biomechanics in Carassius auratus. The model includes the anterior swimbladder, Weberian ossicles, sinus impar, transverse canal, and saccule. Our relatively simple model clearly predicts a phase differential in signals from monopole sources located one meter behind and in front of the fish. This phase differential is believed to play a role in source localization. Moreover, the relative motion between the saccular otolith and sensory epithelium predicted by the model correlates well with auditory thresholds reported in the literature as a function of frequency (i.e., larger relative motion at lower thresholds).

The objectives for the next year are to complete the first round of frequency response measurements on *Carassius auratus* in the 10- 3000 Hz band, and extend the mathematical model to all the peripheral organs and at least three-degrees-of-freedom. Currently, our model indicates that the Weberian ossicles control the response of the periphery down to very low frequencies. The measurements should verify this mechanical behavior. We will continue development of the mathematical model to include the posterior chamber of the swimbladder as well as stiffness and damping in the pinned joints between the Weberian apparatus and vertebrae. We also plan to

incorporate a three-dimensional rigid body model for the saccular and lagenar otoliths, and the micromechanics of the hair cell bundles in the sensory epithelia.

Results of this study will improve understanding of the transduction of acoustical to electrical energy in the peripheral auditory system and the role of the peripheral mechanics in auditory functions, such as source localization. Coupling of the bioelectromechanical model with the peripheral signal processing model being developed by Popper, Fay and Shamma (see below) will provide new understanding of localization mechanisms in the periphery as well as a basis for hardware development of a dual acoustic pressure and particle velocity sensor.

NEAR-FIELD ACOUSTIC DETECTION

P.I.: Ad J. Kalmijn

I am pursuing my studies on the earliest and most basic function of the lateral line and inner ear in the detection of the acoustic near field. The inner-ear sense organs are treated as a set of sophisticated acceleration detectors, whereas the lateral line is considered to detect the acceleration gradient integrated along the lengths of the sensory arrays.

To provide a mathematical and pictorial description of the hydrodynamic-acoustic fields produced by predator and prey, I am developing a comprehensive model, founded in the acoustic wave equation, Laplace's equation, and Green's integral identity. The input of the model are the normal velocities at the surface of the source. The resulting equations are solved using the elegant and highly efficient boundary element method, yielding the desired multipole approximation of the moving object and an exact mathematical representation of the field it produces. The model will be fitted to prescribed or measured surface velocities of imaginary and real biological objects. The field obtained will be verified by measuring the particle accelerations at selected locations in the vicinity of the source subsequent to implementation of a newly developed solid-state pressure-gradient strain-gage transducer.

In an effort to discover the most elementary auditory function of the inner ear, I have recently gained new clarity as to the acceleration stimuli a predator receives in the vicinity of quietly swimming prey. By virtue of the periodic thrust of the tail beat, fishes swim in an accelerated manner, producing genuine acoustic fields. The detection of these accelerations conceivably led to the higher functions of hearing However, fishes are also highly responsive to non-accelerating objects, such as gliding prey. Because of the changes in position relative to the source, the recipient fish is from moment to moment exposed to different particle velocities and therefore experiences also in this case accelerations. Hence, even the most stealthily moving prey can be detected by the acceleration transient imparted to the predator. In the source frame of reference, the two kinds of accelerations may be considered the local derivative and the convective derivative of the velocity, respectively.

To demonstrate the responses of the lateral line and inner ear to the inferred local and convective accelerations, I will, together with Dr. Per Enger, initiate nerve or receptor potential recordings in the intact, freely moving animal. The test fields will consist of real- world implementations of the comprehensive hydrodynamic-acoustic model in progress. The new pressure-gradient accelerometer will be used to calibrate the stimulus fields. The electrophysiological studies will be complemented with behavioral assays to establish the biological significance of the local and convective acceleration stimuli.

SOUND LOCALIZATION BY FISH: MECHANISMS AND MODELS

P.I.'s: Arthur N. Popper, Richard R. Fay, Shihab Shamma

The purpose of the proposed study will be to develop a better understanding of the physiology and functional organization of the auditory periphery in fishes. These results will be applied to developing better computational models to help elucidate the methods by which fishes detect and process low-frequency acoustic signals. Emphasis will be placed upon mechanisms of sound source localization including the determination of the azimuth, elevation, and range of sound sources. We will obtain the first data on directional responses of fully characterized neurons and then apply this information to developing new models for understanding how fish can determine sound source direction and distance.

Specifically, the project will obtain extracellular and intracellular neurophysiological data from neurons innervating the various endorgans of the ear that will be characterized physiologically as well

as ultrastructurally. We will obtain data not only on the response properties of the neurons, but also on the regions of the sensory epithelia they innervate and their central projections. We will record from characterized neurons while the fish is being stimulated using a well-controlled directional stimulus. The stimulus field will be created by a unique system comprised of a 3-dimensional electromechanical shaker system and a loudspeaker in air that controls the sound pressure waveform independently of the particle acceleration waveform. All physiological responses will be interpreted with respect to the actual motion of the animal which will be precisely measured in each case. Stimulus levels will be quite low (peak-peak displacements between 0.1 nanometer and 1 micrometer).

Heretofore there have been only the most limited data on detection of low frequency sounds by fishes and on the ability of fishes to determine the direction and distance of a sound source. While it is known that some species can localize sounds, there are few data on the mechanism(s) involved both peripherally (at the level of the ear) and in the brain. Our investigations will seek to determine the role of the ear and eighth (auditory) nerve in detection and processing of low frequency signals and signals that originate from different locations.

These data are also of fundamental importance for developing refined computational models of sound detection and processing in fishes. Without physiological data on the role of the auditory periphery, we can only speculate on the inputs available to any central computational system. In essence, earlier models of sound source localization in fish have been based only upon the most minimal data, and one of the major gaps has been in knowing the response of the ear to directional stimulation. Our experiments will provide such data and enable the model to more realistically include how the auditory periphery responds to directional signals. Moreover, in collaboration with Dr. Hastings and her group (see above), we will be able to incorporate information about the biomechanical properties of the endorgans into our model. It may also be possible, through collaboration with Dr. Coombs and her colleagues, to incorporate responses of the lateral line into the model.

MODELS FOR THE DIRECTIONAL ACOUSTIC STARTLE REFLEX IN FISH

P.I.: Peter H. Rogers

A model for the Mauthner Cell mediated directional startle reflex in fish has been proposed independently by Eaton and Rogers. The key to the model is the relative *initial* polarity of the pressure and acceleration channel signals. This information is believed to be sufficient to allow the fish to make the right escape "decision" for a wide variety of source types and relative orientations of the fish in both the near field and far field. The model is relatively simple and is predictive as well as explanatory. It should therefore be possible to completely validate the model experimentally. It is hoped that understanding this simple system will serve three purposes relative to the understanding of the more general problem of directional hearing in fish: 1) the algorithms and mechanisms of the auditory Mauthner cell reflex may be duplicated in the CNS to provide directional sensitivity to the reception of impulsive (but small amplitude) acoustic signals; 2) the startle response may explain the function of some of the observed anatomical structure and ultrastructure of the auditory system and 3) the startle mechanism may offer clues to the algorithms used for more general directional hearing tasks. Our efforts will primarily deal with the acoustics and behavioral aspects of validating the model and Eaton's will concentrate on the electrophysiology. By utilizing our large (30,000 gallon) acoustic test tank with two large spherical PZT transducers as sources, we should be able to completely and independently control (and specify) the initial parts of the pressure and acceleration waveforms in the frequency range of interest. We can synthesize any natural (or unnatural) acoustic field conditions in the test region of the tank, determine what the fishes response to that signal is and whether the response is or isn't consistent with the model. By varying the system, (e.g. by flooding the swimbladder or eliminating signals from one or more of the otolith organs or the lateral line) and the field, we should be able to thoroughly test the model.

The general design of the experiments will be as follows. The subject will be contained with sufficient conditioned water in a sealable transparent bag, as the chemicals in the tank water are toxic. The bag material is sufficiently thin and flexible so as to be acoustically invisible. The fish will be placed in the bag underwater to assure that no air is trapped in the bag. This will be lowered to the center of the tank where the acoustic conditions are controlled. The behavioral response of the

subject to stimuli will be monitored using a high speed video camera. Both the vertical and horizontal planes can be recorded on one camera by using an angled mirror, a technique used by Enger, *et al.*). The response to stimuli will be graded against the initial phase of the Mauthner initiated startle response, the 'fast body bend', that lasts about 20 msec. This response was described by Eaton, *et al.* as a short latency, unilateral contraction of the trunk and tail: the fish assuming a C-like shape with both the head and the tail displaced to one side. This can easily be characterized as to the left or right, as the startle response is accompanied by only one M-spike. An independent observer of the video will score the responses. The scores will then be correlated to the stimulus. Since the fish are known to habituate to the stimulus, the interstimulus interval (5-15 min.) will be adjusted to maximize the probability of obtaining responses.

Cobalt ions can be used to temporarily disable the lateral line without affecting the ears. Studies can be made using these techniques to show their involvement in the startle response.

The direct signal at the utricle can be eliminated by removing the otolith or surgically cutting the nerve to the utricular macula. Although less accessible, the saccular-lagenar branch of the auditory nerve can also be severed, as described in Moulton and Dixon. To eliminate the indirect signal, the swim bladder can be removed through a lateral incision or filled with fluid.

In addition to the research described above we also plan to continue our study of scattered ambient noise as an auditory stimulus for fish by testing the hypothesis on a non-ostariophysan fish with a swim bladder and also on a species without a swim bladder. In particular, we need to determine whether or not a non-ostariophysan fish can determine the direction of the scattering fish. We would also like to develop behavioral techniques which could help determine whether or not fish detect and/or localize neighboring fish by imaging scattered ambient noise.